

**The Structure, Development, and Bionomics of
the House-fly, *Musca domestica*, Linn.**

**Part II.—The Breeding Habits, Development, and the Anatomy
of the Larva.**

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With Plates 30—33.

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I. INTRODUCTION.

IN the present paper, which is the second of the series of three, the breeding habits and development of *M. domestica* and the anatomy of the mature larva will be described. Its publication has been delayed owing to the fact that I wished to make the observations on the breeding habits and life-history as complete as possible. With the recent appearance of two short papers by Newstead (1907) and Griffith (1908), many of whose observations, to which I shall refer later, are confirmatory of my own results, we now have a more complete account of the breeding habits of this insect.

The anatomy of the larva has been described in a similar manner to that of the fly (1907). I have refrained in this paper from giving a detailed account of the embryology and the development of the imaginal discs, as these are separate and specialised studies, and would have resulted in too great a digression from the plan originally adopted.

The methods used were the same as those previously employed. The anatomical structures were studied with the aid of the Zeiss binocular dissecting microscope, and the drawings were made from the dissections. The latter were confirmed by means of serial sections. Too much stress cannot be laid on the importance of employing both these methods where possible, as it frequently happens that mistakes are made in investigating by one method only, which would be unrectified were not the other employed in confirmation.

I wish to thank the Council of the Manchester University for providing me with a suitable experimental greenhouse and apparatus for the experimental portion of this investigation; the absence of such facilities would have been a severe handicap. The outdoor observations on the breeding habits have been made during the last few years in Manchester and the surrounding district.

The third paper, which will conclude this study of *M. domestica*, will deal with the bionomics of the fly, its para-

sites and its relation to man, and certain of its allies which frequent houses will be considered.

II. BREEDING HABITS OF *M. DOMESTICA*.

The development of *M. domestica* was first described by Carl de Geer (1776); but, although he stated that it developed in warm and humid dung, he did not give the time occupied by the different developmental stages. He refers to the enormous quantities of flies occurring from July to August. His statement concerning their development is especially interesting, as he appears to be the first investigator who called attention to what I consider to be one of the most important factors in the development of the fly, namely, the process of fermentation occurring in the substance in which development is taking place. He says (p. 76), "*Les larves de cette espèce vivent donc dans le fumier, mais uniquement dans celui qui est bien chaud et humide, ou pour mieux dire qui se trouve en parfaite fermentation*" (the italics are mine). Since the completion of my own investigations on the development, all of which indicated the importance of this factor fermentation, Newstead (l. c.) has come to the same conclusion. The work of Keller (1790), to which reference was made in the first part of this memoir, contains many interesting and careful observations on the breeding habits of the "*Stubenfliege*." He found that the eggs hatched from twelve to twenty-four hours after deposition. He reared the larvæ in decaying grain where, no doubt, fermentation was taking place; also in small portions of meat, slices of melon, and in old broth. His observations are extremely interesting, and, excluding mistakes which were due to the lack of modern apparatus, his account is still a valuable contribution to our knowledge of the subject. Bouche (1834) describes the larvæ as living in horse-manure and fowl-dung, especially when warm. He does not give the time occupied by the earlier developmental stages, but states that the pupal stage lasts from 8—14 days. Packard (1874)

was the next to study the development and working in the United States of America at Salem, Mass., he found that the larvæ emerge from the eggs twenty-four hours after deposition; the times taken by the three larval stages—for he found that there were two larval ecdyses—were: first, about twenty-four hours; the second stage, he thought, was from twenty-four to thirty-six hours; and the third was probably three or four days; the entire larval life being from five to seven days. The pupal stage was from five to seven days, so that in August, when the experiments were carried on, the time from hatching to the exclusion of the imago was ten to fourteen days. Taschenberg (1880) incorporates the work of Keller and Bouche, and does not appear to add anything of importance to the facts already mentioned. He states that the female flies deposit their eggs in damp and rotting food-stuffs, bad meat, broth, slices of melon, dead animals, cesspools, and manure-heaps. He further says that they have also been observed laying their eggs in spittoons and open snuff-boxes. With reference to the last statement, I find that the larvæ will feed on expectorated matter mixed with a solid substance, such as earth, if they are kept warm, though they cannot feed on salivary sections merely; but, although flies might improvidently deposit their eggs in an open snuff-box, the larvæ would soon perish on hatching on account of the dry conditions.

Howard (1896—1906) first studied the breeding habits of the fly in 1895 in Washington, U.S.A., and he described them in 1896, and more fully subsequently. He found that they could be rarely induced to lay their eggs in anything but horse-manure and cow-dung, and that they preferred the former. The periods of development he found were as follows:—from the deposition of the egg to the hatching of the larva about eight hours; the first larval stage one day; second larval stage one day; third larval stage—that is, from the second ecdysis to pupation—three days, and the flies emerged five days after the pupation of the larvæ, thus making the whole period of development about ten days. The same

author in a valuable study of the insect fauna of human excrement (1900), describes experiments in which he was successful in rearing *M. domestica* from human excrement both in the form of loose fæces and in latrines. Newstead (l. c.), in addition to confirming some of my observations, also found the larvæ in spent hops, dirty beddings from rabbits and guinea-pigs, bedding from piggeries, and in the rotten flock beds and straw mattresses which, I suppose, were either in, or from, ashpits, and fouled with excremental products, although it is not stated. He appears to have overlooked some of the work of previous investigators.

My studies of the breeding habits of *M. domestica* were initiated in 1905, and were continued in 1906, when a short account of some of the results was published (1906). The shortest time which I then obtained for the development of any batch of larvæ was twenty days, although, taking the shortest period obtained for each developmental stage in the series of experiments, the development could have been completed in fifteen days under suitable conditions. In the summer of 1907 I continued my experiments on a much larger scale and under better circumstances, and the following are the results of my experiments and outdoor observations :

The larvæ have been successfully reared in horse-manure, cow-dung, fowl-dung, human excrement, both as isolated fæces and in ashes containing or contaminated with excrement, obtained from ashpits attached to privy middens, and such as is sometimes tipped on to public tips. I found that horse-manure is preferred by the female flies for oviposition to all other substances, and that it is in this that the great majority of larvæ are reared in nature ; manure-heaps in stable yards sometimes swarm with the larvæ of *M. domestica*. It was also found that the larvæ will feed on paper and textile fabrics, such as woollen, cotton garments, and sacking which are fouled with excremental products if they are kept moist and at a suitable temperature. They were also reared on decaying vegetables thrown away as kitchen refuse, and on such fruits as bananas, apricots, cherries, plums, and peaches,

which were mixed, when in a rotting condition, with earth to make a more solid mass. Although they can be reared in such food-stuffs as bread soaked in milk and boiled egg, when these are kept at a temperature of about 25° C., I was unable to rear them to maturity in cheese, although they fed on the substances for a few days and then gradually died, my failure may have been due to the nature of the cheese which was used, only one kind being tried. In addition to rearing the larvæ on isolated human fæces, such as are frequently found in insanitary court-yards and similar places, they were found in privy middens, and also on a public tip among the warm ashes and clinker where the contents of some privy middens had also evidently been emptied; I bred the flies out from this material.

III. FACTORS OF DEVELOPMENT.

The rate of development depends primarily on the temperature of the substance on which the larvæ are feeding. This was shown in my experiments in which the larvæ were reared in horse-manure kept in a moist condition in an incubator at a constant temperature of 35° C. At this temperature the development is completed in eight to nine days. I found that a higher temperature of 40° C. was too great for the larvæ as they were simply cooked and perished at such a temperature. This has been confirmed by Griffith (l.c.), who found that the life-history was completed in the same time on incubating at a temperature of about 22°—23° C. I do not think that a shorter time than this for the development—that is, from the deposition of the egg to the emergence of the perfect insect from the pupæ—will ever occur in this country, as we rarely enjoy prolonged spells of hot weather which would bring about such conditions as regards temperature. It is interesting to note that Smith (1907) gives the time of development in horse-manure in India under natural conditions as eight days; he also bred *M. domestica* from an artificial latrine containing human excreta mixed with earth, which confirms

English observations for India. In England, during a period of extremely hot weather, flies might develop in about nine days, but such a rate of development would not usually occur, nevertheless, as I shall show in the concluding part of this memoir, such a contingency must be guarded against. Larvæ reared in the open air in horse-manure which had an average, but not a constant, daily temperature of 22.5° C., occupied fourteen to twenty days in their development according to the air temperature.

The effect of the character of the food on which the rate of development also depends is well shown by a comparison of the times of the developmental periods in two of the experiments where the average daily temperature was practically the same, namely, 19.3° C. and 20.5° C. In the former experiment, in which human fæces were used, the development was completed in twenty days, and in the latter, in which bananas were used, the development occupied twenty-seven days; the time was rather lengthened in both cases by the fact that the larval food was rather dry, but equally dry in both experiments as they were kept together; had more moisture been present the times would probably have been correspondingly shortened.

It was experimentally proved that when larvæ were reared, in batches on the same kind of food material with conditions, as regards temperature the same, the developmental period was longer for those larvæ which were subject to dry conditions than for those subject to moist conditions. In an experiment at an average temperature of 22° C. larvæ reared on horse-manure which was kept in a rather dry condition took thirty days to complete the development, and another batch at the same temperature, but on horse manure which was kept moist, the development was completed in thirteen days. Under similar conditions, with regard to temperature, the rate of development is directly proportional to the condition of the food as regards moisture. Dry conditions not only retarded development in some of my experiments to five and six weeks, but also tended to produce flies of sub-

normal size. Moisture is necessary for the development, and if the food becomes too dry the result is fatal, as the larvæ perish.

A fourth and a most important factor affecting development and one intimately connected with the previous factors—temperature, character of food, and moisture—is that of fermentation, to which reference has already been made. This process appears to take place in the substances on which the larvæ best subsist. Whether the suitability of the food is determined by the nature of its fermentation is a point which I was unable to determine, but which I am inclined to believe. I feel certain, however, that the calorific property of fermentation is the most important part of this process on account of its direct relation to the time of development; the endogenous heat of excremental products and decaying substances acting either in addition to, or independently of, the temperature of the surrounding air is of great advantage in accelerating the rate of development.

The Rate of Development.—This was never found to be less than eight days, and was more usually twelve to twenty days owing to the fact that a continuously high air temperature was not maintained for any sufficient length of time; with such a continuous period of hot weather the development would take about ten to twelve days, and in very great heat might be completed in a day or two less as the internal temperature of the breeding places, such as manure-heaps is usually higher than the temperature of the air. It must be remembered, however, that except by incubation it is difficult to experimentally imitate such natural conditions as occur in a manure-heap or privy midden, where, owing to a larger amount of material, a higher constant temperature is maintained. All experimental results except those of incubation tend to give a long rather than a short rate of development. In many cases where the average temperature was 20° C., but the food material rather dry, the developmental period was about three weeks, and where the temperature was low and the food became dry it extended to

as much as six weeks, the greater time being spent in the pupal state which was sometimes of three or four weeks duration.

In no case was I able to keep the pupæ through the winter as I have been able to keep the pupæ of *Stomoxys calcitrans* and other forms.

My experiments and observations point to the fact that in the presence of suitable larval food, such as excremental matter or decaying and fermenting food materials in a moist and warm condition, the female flies would lay their eggs and the larvæ would develop if the temperature of the air were sufficiently high for the prolonged activity of the flies. In winter this last condition is not naturally satisfied, but under such conditions as are found, for example, in warm restaurants and kitchens, stables and cowsheds, female flies may be often found during the winter. On dissecting such flies I have found mature ova in the ovaries, and living spermatozoa in the spermathecæ, which facts support this view. Griffith (l. c.) has succeeded in rearing batches of eggs in November, December, and early January under artificial conditions, which further proves their ability, given the necessary conditions as regards temperature, to breed during the winter months. In this country *M. domestica* breeds, as a rule, from June to October, and the greatest egg-laying activity prevails in August and September. As I have already contended, and as Griffith has shown, they may breed at other times if the necessary conditions are present; I have obtained eggs from flies caught in restaurants in December; Keller also mentions the fact that he obtained eggs in January. These facts may account for the rapid appearance of flies in the early summer. It is not unlikely that the flies which survive the winter months, which many spend in a dormant condition if they are not fortunate enough to remain active in a warm restaurant or stable, lay their eggs, almost immediately on renewing their activity, in such places as manure-heaps which are kept, as is often the case in towns, under cover, and which are consequently warmer externally than those in the open. In this way a large number of flies

would be reared and ready to assume their customary activity under the benign influence of the sunny days of June.

I have made many experiments with a view to finding out the rapidity with which house-flies breed. Anyone who has endeavoured to keep flies alive in an enclosed space will appreciate the difficulty of the task, those who have not done so would hardly realise it. Fewer insects seem less tenacious of life when enclosed even in a comparatively large enclosure of six or nine cubic feet. It is a remarkable fact, as one would imagine a priori that these insects, flying about everywhere as they do, could be easily kept in a roomy cage if given the necessary food and water. This, however, has not been the case in my experience; the longest period which I have been able to keep them in captivity in summer is seven weeks. I am pleased to find that Griffith has succeeded in keeping a male fly sixteen weeks, and has obtained four batches of eggs from females in captivity. In one of my experiments I was successful in obtaining flies of the second generation bred in captivity. I found that the flies became sexually mature in ten to fourteen days after their emergence from the pupal state and, four days after copulation, they began to deposit their eggs, that is, from the fourteenth day onwards from the time of their emergence.

From these results it may be seen that in very hot weather the progeny of a fly may be laying eggs in about three weeks after the eggs from which they were hatched had been deposited. As a single fly lays from 120—150 eggs at one time and may deposit five or six batches of eggs during its life, it is not difficult to account for the enormous swarms of flies that occur in certain localities during the hot summer months, and algebraical calculations are not required to more vividly impress the fact.

IV. DEVELOPMENT.

As I have already stated, *M. domestica* may become sexually mature in about ten to fourteen days after emer-

gence from the pupal case, and at this time they may be seen copulating.

1. The copulation of *M. domestica* appears to have been first described by Reamur (1738). It has been carefully described recently by Berlese (1902), whose observations my own confirm. The male may perform a few tentative operations before copulation takes place, and these have been mistaken for the actual act. The male alights on the back of the female by what appears to be a carefully calculated leap from a short distance, and this act seems to indicate a faculty on the part of the fly of being able to judge distance. It then caresses the head of the female, bending down at the same time the apical portion of the abdomen. The male fly is, however, peculiarly passive during the operation, its influence apparently being only tactual, it is only when the female exerts her ovipositor and inserts it into the genital atrium of the male that copulation can successfully take place. When the ovipositor has been inserted into the genital atrium of the male, the accessory copulatory vesicles of the female become turgid and retain the terminal segment in this position, in which the female genital aperture is situated opposite to the male genital aperture at the end of the penis, the latter depending from the roof of the genital atrium. (This will be better understood by reference to the figures of these parts in Part I of this Memoir). The attachment of the penis to the female genital aperture is made still firmer by the dorsal sclerites of the eighth segment of the female and the ventral sclerites of the seventh segment, the so-called secondary forceps of the male acting respectively above and below the penis. The fifth ventral segment, or primary forceps of the male, assist the accessory copulatory vesicles of the female in preventing the withdrawal of the ovipositor before the spermatozoa have been injected into the female genital aperture, by which way they enter the spermatheca. The whole act may be over in a few moments or they may remain in coitu for several minutes.

The eggs are laid a few days after copulation; I found

that oviposition may take place as early as the fourth day; Taschenberg (t. c.) states that the female lays on the eighth day after copulation. When about to deposit its eggs the fly alights on the substance which it selects as a suitable nidus and, if possible, crawls down a crevice out of sight. There it lays its eggs in clumps; they are usually placed vertically on their posterior ends and closely packed together. During a single day, if undisturbed, a fly may lay the whole batch of eggs which are mature in the ovaries and which may number, I find from actual count, from 120—150.

2. The Egg.—The egg of *M. domestica* (Pl. 30, fig. 1) measures 1 mm. in length, sometimes slightly less. It is cylindrically oval; one end, the posterior, is broader than the other, towards which end the egg tapers off slightly. The outer covering or chorion is pearly white in colour, the polished surface being very finely sculptured with minute hexagonal markings. Along the dorsal side of the egg are two distinct curved rib-like thickenings having their concave faces opposite. In the hatching of the eggs which I have observed, the process was as follows:—A minute split appeared at the anterior end of the dorsal side to the outside of one of the ribs; this split was continued posteriorly (fig. 2), and the larva crawled out, the walls of the chorion collapsing after its emergence. The time of hatching varies according to the temperature. With a temperature of 25°C.—35°C. the larvæ hatch out from eight to twelve hours after the deposition of the eggs; at a temperature of 15°C.—20°C. it takes about twenty-four hours, and if kept as low as 10°C., two or three days elapse before the larvæ emerge.

3. The Larva.—First larval stage or first instar.—The newly-hatched larva (fig. 8), measures 2 mm. in length. It contains the same number of segments as the mature larva and at the anterior end of the ventral surface of each of the posterior eight segments there is a spiny area (*sp.*). The posterior end is obliquely truncate, and bears centrally the only openings of the two longitudinal tracheal trunks, each trunk opening to the exterior by a pair of small oblique slit-

like apertures situated on a small prominence (*p.sp.*). There are no anterior spiracular processes in the first larval stage. The oval lobes are relatively large and on the internal ventral surface of each there is a small T-shaped sclerite (fig. 13, *t.s.*). These sclerites lie lateral to the falciform mandibular sclerite (*m.s.*). The cephalopharyngeal skeleton of the first larval instar is slender and, in addition to the sclerites already mentioned, consists of a pair of lateral pharyngeal sclerites or plates (*l.p.*) deeply incised posteriorly, forming well pronounced dorsal and ventral processes. The lateral plates are connected antero-dorsally by a curved dorsal sclerite (*d.p.s.*). The anterior edges of the lateral plates are produced ventrally into a pair of slender processes (*h.s.*), the anterior portions of these processes, which represent the hypostomal sclerite, are involute and articulate with the mandibular sclerite. The alimentary canal of the first larval instar is relatively shorter than that of the adult, and consequently it is not so convoluted; the salivary glands are proportionately large.

The first larval instar may undergo ecdysis as early as twenty hours after hatching, but it is usually from twenty-four to thirty-six hours that the ecdysis takes place: under unfavourable conditions with regard to the factors governing the development, the first larval instar sometimes lasted three or four days. Ecdysis begins anteriorly, and the larva not only loses its skin but also the cephalopharyngeal sclerites which are attached to the stomodæal portion of the ecdysed chitinous integument; the chitinous lining of the proctodæal portion of the alimentary tract is also shed.

The second larval stage or second instar. This stage is provided with a pair of anterior fan-shaped spiracular processes similar to those of the mature larva. The posterior spiracular orifices are shown in fig. 12. They are slit-like apertures rather similar to those of the first instar but larger in size. The cephalopharyngeal skeleton is thickened and less slender in form than that of the first instar. It resembles the cephalopharyngeal skeleton of the mature larva except that the posterior sinuses of the lateral pharyngeal

sclerites are much deeper, thus making the dorsal and ventral posterior processes more slender than in the mature larva. The second larval instar may undergo ecdysis in twenty-four hours at a temperature of 25°—35°C., but under cooler conditions or with a deficiency of moisture the period is prolonged and may take several days.

The third larval stage or third instar, which is the last larval stage, grows rapidly. The anatomy of this the mature larva will be fully described. Larvæ incubated at a temperature of 35°C. complete this larval stage and pupate in three to four days, on the other hand, under less favourable developmental conditions, it sometimes extended over a period of eight or nine days. Incubated larvæ cease feeding at the end of the second day of this stage and gradually assume a creamy colour, which colour is due to the large development of the fat body and to the histolytic changes which are taking place internally; larvæ dissected at this stage contain a very large amount of adipose tissue cells. Between the third and fourth day the larva contracts to form the pupa.

4. The Pupa.—The process of pupation may be completed in so short a time as six hours. The larva contracts, the anterior end especially being drawn in, with the result that a cylindrical pupal case is formed (fig. 15), the posterior region being very slightly larger in diameter than the anterior; the anterior and posterior extremities are evenly rounded. The average length of the pupa is 6.3 mm. Owing to the withdrawal of the anterior segments the anterior spiracular processes (*a.sp.*) are now situated at the anterior end, and the posterior spiracles (*p.sp.*) form two flat button-like prominences on the posterior end. The pupa changes from the creamy-yellow colour of the larva to a rich dark brown in a few hours. As the last larval skin has formed the pupal case, it being a coarctate pupa, in addition to the persistence of the spiracular processes the other larval features such as spiny locomotory pads can be seen.

During the first twelve hours or so of pupation the larva loses its tracheal system, which appears to be withdrawn

anteriorly and posteriorly, the latter moiety being the larger; the discarded larval tracheal system lies compressed against the interior of the pupal case (*l.tr.*). Communication with the external air is formed for the nymphal¹ developing tracheal system by means of a pair of temporary pupal spiracles, which appear as minute spine-like lateral projections between the fifth and sixth segments of the pupal case (*n.sp.*). Each of these communicates with a knob-like spiracular process (fig. 10, *n.sp.*) attached to the future prothoracic spiracle of the fly. The proctodæal and stomodæal portions of the alimentary tract are also withdrawn, and with the latter the cephalo-pharyngeal skeleton, which lies on its side on the ventral side of the anterior end of the pupal case.

The histogenesis of the nymph is extremely rapid, so that at the end of about thirty hours, in the rapidly developing specimens, it has reached the stage of development shown in fig. 10, in which most of the parts of the future fly can be distinguished although they are ensheathed in a protecting nymphal membrane. The head, which with the thorax has been formed by the eversion of the cephalic and thoracic imaginal discs from their sacs, is relatively large: two small tubercles (*an.*) mark the bases of the antennæ. The proboscis is enclosed in a large flat sheath which at this period appears to be distinctly divided into labral (*lbr.*) and labial (*lb.*) portions. In a short time the parts of the proboscis are seen to develop in these sheaths (fig. 11). The femoral and tibial segments of the legs are closely adpressed and lie within a single sheath. The wings (*w*) appear as sac-like appendages, and, as the nymphal sheath of the wing does not grow beyond a certain size, the wing develops in a slightly convoluted fashion by means of a fold which appears in the costal margin a short distance from the apex of the wing.

With a constant temperature of about 35° C., or even less, the exclusion of the imago may take place between the third

¹ The word "nymph" is used here to designate that stage in the development which begins with the appearance of the form of the future fly, and ends when the exclusion of the imago takes place.

and fourth day after pupation, but it is more usually four or five days as the larvæ, when about to pupate, leave the hotter central portion of the mass in which they have been feeding and pupate in the outer cooler portions: this outward migration may be a provision for the more easy emergence of the excluded fly from the larval nidus. In some cases the pupal stage lasts several weeks, but I have never succeeded in keeping pupæ through the winter.

When about to emerge, the fly pushes off the anterior end of the pupal case in dorsal and ventral portions by means of the inflated frontal sac, which may be seen extruded in front of the head above the bases of the antennæ. The splitting of the anterior end of the pupal case is quite regular, a circular split is formed in the sixth segment and two lateral splits are formed in a line below the remains of the anterior spiracular processes of the larva. The fly levers itself up out of the barrel-like pupa and leaves the nymphal sheath. With the help of the frontal sac which it alternately inflates and deflates it makes its way to the exterior of the heap and crawls about while its wings unfold and attain their ultimate texture, the chitinous exoskeleton hardening at the same time; when these processes are complete the perfect insect sets out on its career.

V. THE LARVA OF *MUSCA DOMESTICA*.

1. External Features.—The external appearance of the typical acephalous muscid larva or “maggot” (fig. 5) is well known. It is conically cylindrical. The body tapers off gradually to the anterior end from the middle region. The posterior moiety is cylindrical, and except for the terminal posterior segment the segments are almost equal in diameter. The posterior end is obliquely truncate. The cuticular integument is divided by a number of rings; this ringed condition is brought about by the insertion of the segmentally-arranged somatic muscles the serial repetition of which can

be clearly understood by reference to fig. 16. The average length of the full-grown larva of *M. domestica* is 12 mm.

The question as to the number of segments which constitute the body of the muscid larva is a debated subject. I have, however, taken as my criterion the arrangement of the somatic musculature. Newport (1839) considered that the body of the larva of *Musca vomitoria* consisted of fourteen segments, but if the anterior portion of the third segment, that is, my first post-oral segment, is included, there were fifteen, to which view he appeared to be inclined. Counting the anterior segment or "head" as the first, Weismann (1863 and 1864) considers that the body is composed of twelve segments. Brauer (1883) is of the opinion that there are twelve segments, but that the last segment is made up of two; Lowne follows this view in his description of the blow-fly larva and considers that there are fifteen post-oral segments. I am unable to accept Lowne's view. Counting the problematical cephalic segment, for which I shall use Henneguy's (1904) term "pseudo-cephalon," as the first segment, I believe that it is succeeded by twelve post-oral segments, making thirteen body segments in all, which is the usual number for dipterous larvæ as Schiner (1862) has also pointed out. My study of the somatic musculature, as I shall show, indicates the duplicate nature of the apparent first post-oral segment, so that the apparent second post-oral segment (iv), that is, the segment posterior to the anterior spiracular processes, is really the third post-oral segment or fourth body-segment.

The cephalic segment cannot be considered as homologous with the remaining twelve segments, which are true segments of the body as shown by their musculature and innervation. This segment (fig. 9, i), for which Henneguy's term "pseudo-cephalon" is very suitable, probably represents a much reduced and degenerate cephalic segment, its present form being best suited to the animal's mode of life. We may consider the greater part of the cephalic segment of the larva as having been permanently retracted within the head; this is shown by

the position of the pharyngeal skeleton, to the whole of which the name "cephalo-pharyngeal skeleton" has been given. All that now is left of the cephalic segment consists of a pair of oral lobes, whose homology with the maxillæ is very problematical, and at present is not safely tenable. On the dorsal side the oral lobes are united posteriorly. Each bears two conical sensory tubercles (*o. t.*), which are situated, the one dorsally, and the other anterior to this and almost at the apex of the oral lobe. The ventral and ventro-lateral surfaces of the oral lobes are traversed by a number of channels, which will be described later.

The post-cephalic segment, which is composed of the first and second post-oral segments and represents the second and third segments of the body, is conical in shape. The first post-oral segment (ii), to which Lowne gave the name "Newport's segment," is limited posteriorly by a definite constriction and is covered with minute spines. The second post-oral segment bears laterally at its posterior border the anterior spiracular processes (*a. sp.*) The remaining segments of the body—four to twelve—are on the whole similar in shape. At the anterior edge of the ventral side of each of the sixth to twelfth body-segments there is a crescentic pad (fig. 5, *sp.*) bearing minute and recurved spines; these are locomotory pads by means of which the larva moves forwards and backwards. It is important to note that these pads are situated on the anterior border of the ventral side of each segment as they do not appear to have been carefully placed in the previous figures of this species. In addition to these spiniferous pads there are two additional pads of a similar nature, one on the posterior border of the ventral side of the twelfth body-segment, and the other posterior to the anus.

The terminal or thirteenth body-segment is obliquely truncate, but the truncate surface, which occupies more than half the posterior end of the larva, is not very concave as in the blow-fly larva. It bears in the centre the two posterior spiracles (fig. 3, *p. sp.*), which are described in detail with the tracheal system. On the ventral side of the terminal segment

are two prominent anal lobes (fig. 5, *an. l.*), which are important agents in locomotion.

The cuticular integument is thin and rather transparent, so that in the younger larvæ many of the internal organs can be seen through it. In older larvæ the fat-body assumes large proportions and gives the larva a creamy appearance, obscuring the internal organs. The cuticle (fig. 14) is composed of an outer rather thin layer of chitin (*ct.*), which is continuous with the chitinous intima of the tracheæ, and also with the chitinous lining of the stomodæal and proctodæal regions of the alimentary tract. Below this layer there is a thicker layer of chitin (*ct.'*), which does not stain so deeply. In places this lower layer is penetrated by the insertions of the muscles. The cuticle lies on a layer of stellate hypodermal cells (*hy.*), which are well innervated, and attain a large size in the posterior segments of the body.

2. MUSCULAR SYSTEM.

The muscular system of the larva (Pl. 31, fig. 16) consists of a segmental series of regularly repeated cutaneous muscles, forming an almost continuous sheath beneath the skin, together with a set of muscles in the anterior segments of the body which control the cephalo-pharyngeal sclerites and pharynx. In addition to this there are a set of cardiac muscles and the muscles of the alimentary tract.

I have been unable to find a detailed description of the muscular system of the muscid larva, and I do not think that Lowne's excuse for dismissing the cutaneous muscles of the blow-fly larva with a very brief statement, because "the details possess little or no interest," was justified, considering how little is known about the muscular systems of insect larvæ, and constant reference to the classic work of Lyonet (1762) on the caterpillar is not sufficient to satisfy the inquiring student of to-day. The muscular system of the larva, therefore, will be described in some detail.

Muscles of the body-wall.—The cutaneous muscles

are repeated fairly regularly from segments (by segments I mean body-segments) four to twelve and a detailed description of the muscles of one of these segments will serve for the rest. The muscles, though continuous in most cases from segment to segment, are attached to the body-wall at the junction of the segments. The most prominent muscles are the dorso-lateral oblique recti muscles. In segments six to twelve there are four pairs each of external (*ex. d. l.*), and internal dorso-lateral oblique recti (*in. d. l.*) muscles; in segments four and five there are five pairs of external and six pairs of internal dorso-lateral oblique muscles. Ventral to these muscles are four pairs of longitudinal ventro-lateral muscles (*l. v. l.*); the muscle bands of the two more ventral pairs are double the width of those of the two more lateral pairs. In the fifth segment there is only one of the more lateral pairs of the longitudinal ventro-lateral muscles present, and in the fourth segment only the two more ventral pairs remain. In addition to these muscles there are two other pairs of oblique recti muscles; these are, a pair of ventro-lateral oblique muscles (*v. l. o.*) and a pair of internal lateral oblique muscles (*i. l. o.*); both of these are absent in the segments anterior to the sixth. The foregoing muscles, namely the dorso-lateral oblique, the internal lateral oblique, the ventro-lateral oblique and the longitudinal ventro-lateral, by their contraction, bring together the intersegmental rings and so contract the body of the larva.

Attached externally to the anterior ends of the longitudinal ventro-lateral muscles are a number of pairs of ventral oblique muscles (*v. o.*); they vary in number from two to eight pairs in each segment. The number increases posteriorly from two pairs in segment four to four pairs in segment five, five pairs in segment seven, seven pairs in segment ten, eight pairs in segment eleven; the number of pairs then decreases to six or seven pairs in segment twelve. The more ventral pairs of these muscles are not attached at their posterior ends to the intersegmental ring but to the ventral wall of the segment and no doubt assist in bringing forward the ventral spiniferous pads. In segments four to twelve there are three pairs of

lateral muscles (*l. m.*) situated next to the hypodermis and attached in a dorso-ventral position; these will assist in drawing the dorsal and ventral regions of the segments together and so increase the length of the larva. Between segments four and five and the remaining segments to twelve there is, on the intersegmental ring, a pair of lateral intersegmental muscles (*l. i. m.*); these by their contraction bring about a decrease in the size of the intersegmental ring and so assist the lateral muscles in increasing the length of the larva.

The muscles of the last segment (xiii) are not regularly arranged as in the preceding segments; they consist of three main groups: (1) the recti muscles, which assist in contracting the segments; (2) the anal muscles (*an. m.*), which are attached ventrally to the anal lobes (*an. l.*); and (3) the dorso-ventral muscles (*d. v.*), which by their contraction assist in lengthening the segment. In addition to these there are certain small muscles in relation with the posterior spiracles.

In the second and third segments the recti muscles are reduced to four pairs and the attachment of the two lateral and external pairs of muscles has led me to regard the apparently single first post-oral segment as consisting of two segments; it is not a single post-cephalic or pro-thoracic segment as it has been called. There is quite a distinct internal division and the external constriction has been already noticed. This view does not necessarily alter the homology of the third segment, which may still be regarded as pro-thoracic if this is desirable. The segment which I regard as the second body-segment may be a rudiment of the cephalic region which has been almost lost, and this loss, or, as I prefer to regard it, this withdrawal of the head, only serves to make any discussion as to the homologies of these anterior segments with those of the adult extremely difficult, and, I believe, at present valueless. Further, comparative studies of the larvæ of the calyprate muscidæ are necessary before we can arrive at any definite conclusions concerning the composition of the bodies of these larval forms.

The cephalo-pharyngeal muscles (fig. 19).—These muscles consist of four sets: (1) The cephalic retractor muscles, which by their contraction draw the anterior end of the larva and the pharyngeal mass inwards; (2) the protractor and depressor muscles of the pharyngeal mass; (3) the muscles controlling the mandibular, dentate, and hypostomal sclerites; and (4) the internal pharyngeal muscles.

There are four chief pairs of cephalic retractor muscles, of which the two ventral pairs are by far the largest. The more ventral of these two pairs (*v'. c. r.*) arises on the ventral side from the posterior end of the sixth segment, internal to the ventro-lateral longitudinal muscles; the other pair (*v. c. r.*), which is double, arises more laterally from the posterior end of the fifth segment. The remaining pairs of cephalic retractors arise from the posterior end of the third segment. All the cephalic retractor muscles are inserted anteriorly into a ring, the cephalic ring (*c. r.*), on the anterior border of the second segment, the first post-oral segment.

There are two pairs of cephalo-pharyngeal protractor muscles, a dorsal (*d. c. p.*) and a ventral pair (*v. c. p.*). Both are rather broad fan-shaped muscles inserted by their broad ends in the middle of the third segment, slightly to the sides of the dorsal and ventral median lines respectively. The dorsal and ventral muscles of each side are inserted together on the dorso-lateral region of the posterior end of the pharyngeal mass. The pair of depressor muscles (*d. m.*) which are situated dorsally, are attached by their broader ends to the intersegmental ring between segments three and four. They are inserted on to the posterior end of the dorsal side of the pharyngeal mass; by their contraction the posterior end of the pharyngeal mass is raised, the result being that the sclerites articulated to its anterior end are depressed.

There remain six pairs of muscles controlling the mandibular, dentate and hypostomal sclerites, one pair controlling the two foremost sclerites and four pairs controlling the hypostomal sclerite. The mandibular extensor muscles (*m. e.*) are attached to the body-wall in the third segment on each side

of the median line and between the dorsal cephalo-pharyngeal protractors. They are inserted on to the dorsal side of the mandibular sclerite (*m. s.*); by their contraction they elevate the sclerite. This sclerite is depressed by the contraction of a pair of muscles which control the dentate sclerites (*d. s.*), the latter fitting into a notch on the ventral side of the mandibular sclerite. The mandibular depressor muscle (*m. d.*) is attached to the posterior ventral process of the lateral pharyngeal sclerite by the three bands into which the posterior portion of the muscle is divided; the anterior and single end of the muscle is inserted on the ventral process of the dentate sclerite. Four pairs of muscles (*s. d.*) are inserted on the hypostomal sclerite (*h. s.*). Two more dorsal pairs are attached to the intersegmental ring between segments three and four as shown in fig. 16. The two more ventral pairs are attached to the lateral pharyngeal sclerites, one being attached to the ventral side of the posterior dorsal process and the other to the ventral process beneath the mandibular depressor. These muscles, which I call the stomal dilators, are inserted on the sides of the hypostomal sclerite. Their function is, I believe, to open and close the anterior pharyngeal aperture and so control the flow of fluid food into the pharynx and of the salivary secretion; the lowest pair of muscles may be more directly concerned with the latter.

The pharyngeal apparatus is controlled, as in the adult fly, by a series of muscles. In the larval stadium, however, where so large an amount of food is required for the growth and building up of the future insect, there is a greater development and elaboration of the pharyngeal apparatus, including the muscles. In the greater anterior region of the pharynx, that is, the part lying within the pharyngeal sclerites (fig. 18), the muscular system consists of two bands of oblique muscles (*o. ph.*) arranged in pairs. The muscles are attached dorsally to the inside dorsal edges of the lateral plates (*l. p.*) and ventrally to the roof of the pharynx (*r. ph.*), the ventral attachment being more posterior than the dorsal. The posterior region of the pharynx, which is between the lateral plates and

the œsophagus (fig. 17), is controlled by two sets of muscles. Two pairs of elongate oblique muscles (*e. o. m.*) are attached dorsally to the dorsal edges of the lateral plates (*l. p.*) and inserted ventrally on to the roof of the pharynx; these muscles assist the previously described oblique pharyngeal muscles in raising and depressing the roof of the pharynx. They are assisted in enlarging and contracting the lumen of the posterior part of the pharynx by a number of semi-circular dorsal muscles (*s. d. m.*), which by their contraction make the floor of the pharynx more concave, and it is these muscles, I believe, that are chiefly concerned in the maintenance of the peristaltic contractions of the pharynx, by means of which the fluid food, which has been sucked into the mouth by the pumping action of the pharynx, is carried on to the œsophagus.

The similarity between the pharyngeal apparatus of the fly, that is, of the fulcrum and that of the larva, is very striking, both with regard to the form of the skeletal structures and the musculature. If the pharynx of the larva were regarded as being homologous to that of the fly it would further support the view that the head of the larva had been permanently withdrawn into the succeeding anterior body-segments. These structures, however, may be merely analogous; the similarity of structure may have been brought about by similarity of function. Both larva and adult subsist on fluids which are sucked into the mouth and pumped into the œsophagus.

The series of muscular actions which takes place during locomotion appears to be as follows. By the contraction of the pharyngeal protractors the anterior end of the larva is extended, the mandibular sclerite being extended at the same time by the contraction of the mandibular extensor muscles. The mandibular sclerite is now depressed by the contraction of the mandibular depressors, and anchors the anterior end of the larva to the substance through which it is moving. A series of segmental linear contractions now takes place, initiated by the large cephalic retractor muscles, and carried on posteriorly from segment to segment by the

dorso-lateral oblique, the internal lateral oblique, the longitudinal ventro-lateral, the ventro-lateral oblique and ventral oblique muscles. Each segment as it comes forward takes a firm grip ventrally by means of the spiniferous pad. By the time the last spiniferous pad has become stationary the mandibular sclerite has left its anchorage, and by the contraction of the lateral and intersegmental muscles, which takes place from before backwards, the lengths of the segments of the larva are increased serially and the anterior end begins to move forward again, when the whole process is repeated.

3. NERVOUS SYSTEM.

The central nervous system of the larva (Pl. 32, fig. 23) has attained what would appear to be the limit of ganglionic concentration and fusion. The boat-shaped ganglionic mass, which lies partly in the fifth segment, but the greater portion in the sixth segment, is a compound ganglion and represents the fusion of eleven pairs of ganglia similar to that which Leuckart (1858) describes in the first larval stage of *Melophagus ovinus*, but which, however, has not undergone so great a degree of concentration as in *M. domestica*. This ganglionic mass, which for convenience and brevity I shall call the ganglion (Lowne's "neuroblast") does not exhibit externally any signs of segmentation, the interstices between the component ganglia being filled up with the cortical tissue, whose outer wall forms a plain surface. In horizontal and sagittal sections, however, the component ganglia can be recognised and their limits are more clearly defined. The ganglion is surrounded by a thick ganglionic capsular sheath which is richly supplied with tracheæ, and appears to be continuous with the outer sheath of the peripheral nerves. Two pairs of large tracheæ (fig. 24) are found entering the ganglionic sheath, an anterior pair (*tr.* ') which runs in between the cerebral lobes, and a lateral pair (*tr.* ") entering the ganglion beneath these lobes. In the young larva the cortical

layer of cells is proportionately much thicker. The cortical tissue is made up of cells of varying sizes, but which can be grouped in two classes—smaller cortical cells and larger ganglionic cells. Most of the ganglionic cells appear to be unipolar, but there are many of a bipolar and multipolar nature present; they stain readily and possess fairly large nuclei. These ganglionic cells are arranged segmentally, and occur near the origin of the nerves. In the posterior region of the ganglion, where the nerves arise in close proximity, the ganglion cells are very numerous, relatively few of the cortical cells being found. A further demarcation of the component ganglia is brought about by median and vertical strands of the ganglionic sheath-tissue, which perforate the compound ganglion and occur as vertical strands along its median line. Tracheæ also penetrate the ganglion with these strands of capsular tissue.

On the dorsal side of the anterior end of the ganglion is situated a pair of spherical structures (*c. l.*), which may be termed the "cerebral lobes." They are united in the median line dorsal to the foramen traversed by the œsophagus (*oe.*). These cerebral lobes are chiefly of an imaginal character, and contain the fundamentals of the supra-œsophageal ganglia and also of the optic ganglia of the future fly (fig. 27). Each is surrounded by a thin membranous sheath (*sh.*) and is connected with the major cephalic imaginal discs by the optic stalk (*o. s.*).

The nerves arising from the ganglion may be divided into three groups, according to their origin. Eleven pairs of nerves (fig. 24, 1-11) corresponding to the eleven pairs of ganglia arise, two from the anterior end and nine from the sides of the ganglion. Three pairs of nerves (*a.*, *b.* and *c.*) arise laterally from the stalks of the pro-thoracic and meso-thoracic imaginal discs. In the median dorsal line of the posterior half of the ganglion a single pair (*d. a.*') and two median unpaired (*d. a.*" *d. a.*''') nerves have their origin; these are accessory nerves.

The first pair of the two anterior pairs of nerves runs

forward and innervates the posterior region of the pharyngeal mass; the anterior region of the latter is supplied by the second pair of nerves. These nerves also innervate the anterior segments of the body. The first (*a*) of the three pairs of nerves which arise from the stalks of the imaginal discs runs to the anterior end supplying the protractor and retractor muscles of the pharyngeal mass. The second (*b*) of these three pairs of nerves innervates the muscles of the body-wall of the third and fourth segments; the latter segment is also innervated by the third (*c*) of the three pairs of nerves. The succeeding nine pairs of lateral nerves are segmentally distributed, and innervate the muscles of the body-wall of segments five to thirteen. Each nerve bifurcates on reaching the muscles, and these branches further subdivide into very fine nerves.

The nerves, which arise dorsally, and which I have called the accessory nerves, are interesting. The first pair (*d. a.*) which arises about mid-way along the dorsal side of the ganglion, accompanies the pair of nerves supplying the seventh segment. The second (*d. a.*'), which is an unpaired nerve, bifurcates in the seventh segment, and the resulting nerves proceed to the body-wall in association with the nerves supplying the eighth segment. The third and posterior dorsal accessory nerve (*d. a.*'') bifurcates in the seventh segment. Each of the resulting nerves undergoes a second bifurcation; the dextral nerve, bifurcating in the eighth segment, accompanies the nerves supplying the ninth segment; the sinistral nerve bifurcates between segments eight and nine, and the resulting nerves proceed to the tenth segment. None of the remaining lateral nerves appear to be accompanied by an accessory nerve, of which there are four pairs only. The ganglionic sheath is penetrated by tracheæ, some of which arise from the ganglion in association with the nerves which they accompany to the body-wall. Two of these tracheæ are shown (fig. 24, *t.*). Similar fine tracheæ arise with the three posterior pairs of lateral nerves, and on account of their similarity to accessory nerves I at first

mistook them for such, even when dissecting with a magnification of sixty-five diameters, until my serial sections showed their real nature. Without sections it is impossible to distinguish these fine unbranching tracheæ from accessory nerves. I have mentioned this fact as showing the necessity of supplementing the one method by the other.

The visceral or stomatogastric nervous system (Pl. 31, fig. 20) consists of a small central ganglion (*c. g.*) lying on the dorsal side of the œsophagus, immediately behind the transverse commissure of the cerebral lobes from the bases of which two fine nerves are given off to join a fine nerve from the ganglion, which runs dorsally towards the anterior end of the dorsal vessel. A fine nerve from the ganglion runs forward on the dorsal side of the œsophagus towards the pharynx. A posterior nerve (fig. 24, *v. n.*) runs from the ganglion along the dorsal side of the œsophagus to the neck of the proventriculus, where it forms a small posterior ganglion (fig. 20, *pv. g.*), from which fine nerve-fibres arise and run over the anterior end of the proventriculus.

Sensory organs.—The only sensory organs which the larva possesses are the two pairs of conical tubercles (fig. 9, *o. t.*), which have been described already on the oral lobes. In section each consists of an external transparent sheath of the outer cuticular layer; beneath this and surrounded by a chitinous ring are the distal cuticularised extremities of a number of elongate fusiform cells grouped together to form a bulb. These are nerve-end cells and their proximal extremities are continuous with nerve-fibres by means of which they are connected to the ganglion. Both sensory organs of each oral lobe are supplied by the same nerve from the second of the two anterior nerves. Judging from their structure these organs appear to be of an optical nature, and this is the usual view which is held with regard to their function. They would appear merely to distinguish light and darkness, which, for such cryptophagous larva, is no doubt all that is necessary. The negative heliotropism of the larva of the blow-fly has been experimentally proved by Loeb (1890), and my own

observations confirm the same for the larvæ of *M. domestica*.

The hypodermal cells are well innervated and the body-wall appears to be highly sensitive.

4. THE ALIMENTARY SYSTEM.

The alimentary tract increases in length at each of the larval ecdyses, and in the mature larva (Pl. 33, fig. 29), its length is several times greater than the length of the larva. The great length of the alimentary tract of the larva compared with that of the fly is probably accounted for by the fact that a large digestive area is necessary for the rapid building up of the tissues from fluid food which takes place during the larval life. It is divisible into the same regions as the alimentary tract of the mature insect, but it differs from the latter in several respects; these regions are parts of the original stomodæal, mesenteric and proctodæal regions of which the mesenteric is by far the longest in this larva. The regions of the alimentary tract which are derived from the stomodæum and proctodæum are lined with chitin of varying thickness which is attached during life to the epithelial cells, but is shed when the larva undergoes ecdysis. The mesenteron does not appear to be lined with chitin as it is in some insects, in which cases the chitinous intima usually lies loose in the lumen; it is, however, in the larva of *M. domestica*, usually lined with a lining of a mucous character. The whole alimentary tract is covered by a muscular sheath of varying thickness.

The mouth (fig. 6, *m.*) opens on the ventral side between the oral lobes. The ventral and ventro-lateral sides of the oral lobes are traversed by a series of small channels (fig. 14, *ch.*), which are made more effective by the fact that one side of the channel is raised and overhangs the other so as to partially convert the channels into tubes rather comparable to the pseudo-tracheæ of the oral lobes of the fly, to which they have a similar function: the liquid food runs along these

channels to the mouth. Distally many of the channels unite ; the resulting channels all converge and run into the mouth. The anterior border of the oral aperture is occupied by the mandibular sclerite (*m. s.*), and the posterior border is bounded by a lingual-like process (*l.*) that is bilobed at its anterior extremity.

Cephalo-pharyngeal sclerites (Pl. 30, fig. 4).—The sclerites associated with the cephalo-pharyngeal region are rather similar to those of the second larval instar ; they are, however, of a more solid and of a thicker character. Between the oral lobes is seen the median uncinatè mandibular sclerite (*m. s.*). The homology of this sclerite is obscure. Lowne regarded it as being the labrum ; some authors consider that it represents the fused mandibles. As we know at present so little of the comparative embryology of these larvæ it will be best to retain the name by which it is generally known. The basal extremity of the mandibular sclerite is broad, and at each side a dentate sclerite (*d. s.*) is articulated by means of a notch in the side of the mandibular sclerite, the function of which has been shown already in describing the muscles. The mandibular sclerite articulates posteriorly with the hypostomal sclerite (*h. s.*). This consists of two irregularly-shaped lateral portions united by a ventral bar of chitin ; it is anterior to this bar of chitin that the salivary duct opens into the front of the pharynx. The sides of the hypostomal sclerite articulate with two processes on the anterior edge of the lateral pharyngeal sclerites (*l. p.*). The lateral pharyngeal sclerites or plates recall the shape of the fulcrum of the adult fly. Each is wider posteriorly than anteriorly, and the posterior end is deeply incised ; at the base of this incision the nerves and tracheæ which supply the interior of the pharynx enter. The lateral sclerites vary in thickness, as will be seen in the figures of the sections of the pharynx. They are united dorsally at the anterior end by a dorsal sclerite (*d. p. s.*), and ventrally they are continuous with the floor of the pharynx.

The pharynx (Pl. 31, figs. 17 and 18) in certain respects is

similar to that portion of the pharynx of the fly which lies in the fulcrum. The whole length of the floor of the pharynx is traversed by a series of eight grooves separated by bifurcating ribs which are T-shaped in section (fig. 18, *t. r.*), and are called the "T ribs" by Holmgren (1904); they form a series of eight tubular grooves. Holmgren believes that they may have been derived from a condition similar to that found in the pharynx of the larva of *Phalacrocer*, where the floor of the pharynx is traversed by a number of deep but closed longitudinal fissures. These pharyngeal grooves probably have a straining function, but they may also be of use in allowing a certain amount of the salivary secretion to flow backwards towards the œsophagus. The musculature and action of the pharynx has been described. On the dorsal side of the pharyngeal mass and attached laterally to the layer of cells covering the lateral sclerites there is a loose membrane (*m.*), whose function, I believe, is to accommodate the blood contained in the pharyngeal sinus (*p.s.*) when the roof of the pharynx is raised. Posteriorly the floor of the pharynx curves dorsally and opens into the œsophagus.

The œsophagus (fig. 29, *œ.*) is a muscular tube beginning at the posterior end of the pharyngeal mass. It describes a dorsal curve when the larva is contracted, and then runs in a straight line through the œsophageal foramen between the cerebral lobes of the ganglionic mass and dorsal to the ganglion to the posterior region of the sixth larval segment, where it terminates and opens into the proventriculus. It is of a uniform width throughout and is lined by a layer of flat epithelial cells (fig. 25, *œ. ep.*) whose internal faces are lined by a chitinous sheath (*ch. i.*), which is thrown into a number of folds. There is nothing of the nature of a ventral diverticulum forming a crop such as Lowne describes in the larva of the blow-fly.

The proventriculus (fig. 29, *pv.*) varies slightly in shape according to the state of contraction of the alimentary tract; in the normal condition it is cylindrically ovoid and its axis is parallel with that of the body. As will be seen from the

figure (fig. 25), it is rather similar to the proventriculus of the imago in general structure. The œsophageal epithelium penetrates a central core which is composed of large clear cells (*c. c.*); its lumen, being œsophageal, is lined with chitin. This core is surrounded by an outer sheath, the cells (*e. v.*) of which are continuous with those of the ventriculus. At the junction of the central core with the outer sheath of cells there is a ring of small more deeply-staining cells (*i. c.*). This ring was regarded by Kowalevski (1887) as the rudiment of the stomodæum of the nymph, but Lowne is of the opinion that it develops in the nymph into the proventriculus of the imago. I believe that it forms a portion, at least, of the proventriculus of the imago, as it exhibits a very close resemblance to the ring of cells in this region figured in the section of the proventriculus of the imago (fig. 20 of Part I).

The mesenteron of the mature larva is of very great length, and is not divisible into the two regions of ventriculus and small proximal intestine as in the imago, but appears to have the same character throughout; hence Lowne calls it the "chyle-stomach," which term, or ventriculus (fig. 29, *v.*), may be used to designate the whole region from the proventriculus to the point at which the malpighian tubes arise. It is very much convoluted and twisted upon itself. The course of the ventriculus is almost constant, and can be better understood from the figure than from any detailed description. At the anterior end four tubular cæca (*c. v.*) arise. Their walls consist of large cells whose inner faces project into the lumen of the glands; these glands were not present in the imago. The epithelium of the ventriculus (fig. 30) is composed of large cells (*e. v.*), which project into the lumen of the alimentary tract; they possess large nuclei and the sides of the cells facing the lumen have a distinct striated appearance, which is absent in those epithelial cells covered with a chitinous intima. This striated appearance may be related in some way to the production of the mucous intima which is generally present in the ventriculus, and which appears to take the place of the loose chitinous intima or peritrophic

membrane which occurs in this region in numerous insects, and which has been studied in detail by Vignon (1901) and others. Below the epithelial cells a number of small cells (*g. c.*) are found, which may be either gland cells or young epithelial cells. In addition to these cells small groups of deeply-staining fusiform cells (*i. c.*) are found below the epithelium. These, I believe, are embryonic cells from which the mesenteron of the imago arises. The Malpighian tubes arise in the tenth segment at the junction of the ventriculus and the intestine.

The intestine (fig. 29, *int.*) is narrower than the ventriculus and runs forwards as far as the eighth segment, where it bends below the visceral mass and runs posteriorly, to become dorsal again behind the tenth segment, from whence it runs backwards, turning ventrally behind the visceral mass to become the rectum. The epithelium is thrown into a number of folds and is covered with a chitinous intima.

The rectum (*r.*) is very short and muscular, and the chitinous intima is fairly thick and continuous with the outer cuticular layer of the chitinous integument. It is almost vertical and opens by the anus on the ventral side of the terminal larval segment between the two swollen anal lobes.

Salivary glands.—There is a pair of large tubular salivary glands (*s. gl.*) lying laterally in segments five and six. Anteriorly each is continued as a tubular duct; the two ducts approach each other and join beneath the pharyngeal mass to form a single median duct (fig. 19, *sal. d.*) which runs forward and opens into the pharynx on the ventral side as already described. The glands are composed of large cells (fig. 21), which project into the lumen of the gland; they stain deeply and have large active nuclei. The salivary secretion, apart from the digestive properties which it has, is no doubt of great importance in making the food more liquid, as is also the case in the imago, and so rendering it more easy for absorption.

The Malpighian tubes (fig. 29, *m. t.*) arise at the junction of the ventriculus and intestine in the tenth segment. A short

distance from their origin they bifurcate and the resulting four tubules have a convoluted course, being mingled to a great extent with the adipose tissue. They are similar in appearance and histologically to those of the imago, consisting of large cells, of which only two can be seen usually in section; they consequently give the tubules a moniliform appearance. In the mature larva these cells appear to break down to form small deeply-staining spherical bodies. This histological degeneration begins at the distal ends of the tubules, which in the mature larva usually have the appearance shown in fig. 28 (*m. t.*); all the stages of degeneration can be traced out. This process may be a means of getting rid of the remaining larval excretory products.

The four cæca at the anterior end of the ventriculus have already been described.

5. THE RESPIRATORY SYSTEM.

The tracheal system (fig. 26) of the adult larva consists of two longitudinal tracheal trunks united by anterior and posterior commissures, and communicating with the exterior by anterior and posterior spiracles, the latter are situated in the middle of the oblique caudal end, and the anterior spiracles, which are not present in the first larval instar, are situated laterally at the posterior border of the third body-segment.

I believe that the anterior spiracles (*a. sp.*) are true functional spiracles, though for some time I shared Lowne's opinion that they were not functional. This latter view was due to the fact that it was difficult to understand how these spiracles could obtain air when they are immersed, as they usually are, in the moist fermenting materials on which the animal feeds. A careful examination of their structure, however, strengthens my belief that they are able, if necessary, to take in air; the occasions when this is possible are probably not infrequent. Each of the anterior spiracular processes consists of a fan-shaped body (fig. 9, *a. sp.*) bearing six to eight small papilliform processes. The papillæ (fig. 7)

open to the exterior by a small pore which leads into a cavity having a clear lumen surrounded by branched cuticular processes, whose function is probably to prevent solid particles from penetrating the spiracular channel. The body of the fan-shaped spiracular process is filled with a fine reticulum of the chitinous intima, which Meijere (1902) calls the "felted-chamber" (Filzkammer); through this meshwork the air can pass to the longitudinal tracheal trunk.

The posterior spiracles (fig. 3, *p. sp.*) are D-shaped with the corners rounded off and their flat faces are opposed. Each consists of a chitinous ring having internal to the flat side a small pierced knob. Each chitinous ring encloses three sinuous slits, guarded by inwardly-directed fine dendritic processes; through these slits the air enters the small spiracular atrium, one of which is situated internal to each of the spiracles. The spiracular atria communicate directly with the longitudinal tracheal trunks.

The course and origin of the branches of each of the longitudinal tracheal trunks (fig. 26 *l. tr.*) is the same, so that of the left side will be described only. Immediately behind the spiracular atria the short posterior tracheal commissure (*p. com.*) connects the two trunks. In the younger larvæ this commissure is situated more anteriorly, but in the adult it is situated so far back and so close to the spiracles that its presence might easily be overlooked. On the outer side of the tracheal trunk a large branch arises; this, the visceral branch (*v. tr.*), bends ventrally to the lateral trunk, and thus becoming internal to it enters the convoluted visceral mass with its fellow of the other side. The visceral branches extend anteriorly as far as the seventh segment. In the twelfth and thirteenth segments the lateral tracheal trunk has a double appearance. A dorsal and a ventral branch arise in most of the segments, the dorsal branch chiefly supplies the fat body, and the ventral branch supplies the viscera; both give off branches to the muscular body wall. The anterior commissure (*a. com.*) is situated in the fourth segment. It crosses the œsophagus immediately behind the pharyngeal mass. On

the internal side of the portion of the lateral tracheal trunk that is anterior to the commissure a branch arises, and running ventral to the pharyngeal mass it supplies the anterior end of the larva and the oral lobes. A branch that supplies the muscles of this region is given off external to the origin of the anterior commissure. Internal to the origin of the commissure two tracheæ arise; the anterior branch enters and supplies the pharyngeal mass, and the posterior branch (*tr.*') enters the ganglion ventral to the cerebral lobes. In the fifth segment another internal tracheal branch enters the ganglion (*tr.*''). These tracheæ which supply the ganglion appear to run chiefly in the peripheral regions, where they divide into a number of branches, the fate of some of these being interesting. These branches are extremely fine, and they arise, as I have previously mentioned, in association with a number of the segmental nerves with which they run to the body wall.

6. THE VASCULAR SYSTEM AND BODY CAVITY.

The relations and structure of the vascular system of the larva are on the whole similar to those of the fly; there are, however, a number of modifications.

The dorsal vessel, which includes the so-called "heart," is a simple muscular tube lying on the dorsal side immediately beneath the skin, and extending from the posterior tracheal commissure to the level of the cerebral lobes of the compound ganglion in the fifth segment. Its wall is composed of fine striated muscle-fibres arranged transversely and longitudinally, but chiefly in the latter direction. The swollen posterior region (Pl. 33, fig. 31), which is called the heart, lies in the last three or four segments, its anterior limit being hard to define. It consists of three distinguishable chambers, which, however, are not divided by septa. Three pairs of ostia (*os.*), each provided with a pair of internal valves (*v.*); are situated laterally, and place the cardiac cavity in communication with the pericardium, in which this portion of the dorsal vessel lies. There are three pairs of alar muscles controlling the

action of this posterior cardiac region of the dorsal vessel. Lowne describes other openings in the wall of the "heart" of the blow-fly larva, but I have been unable to find others than those already described in this larva; it has three pairs only.

The dorsal aorta is the anterior continuation of the dorsal vessel, which gradually diminishes in diameter. When it reaches the fifth segment and lies above the ganglion, it terminates in a peculiar cellular structure (fig. 24, *c. r.*), which in the blow-fly has a circular shape and was called by Weismann the "ring." In the larva of *M. domestica* it has not so pronounced a ring-like appearance, but is more elliptically compressed and rather Λ -shaped. The cells of which it is composed have a very characteristic appearance, and are rather similar to a small group of cells lying on the neck of the proventriculus and at the anterior end of the dorsal vessel of the fly. From the lower sides of this cellular structure (fig. 28, *c. r.*) the outer sheaths of the major cephalic imaginal discs depend, and extend anteriorly to the pharyngeal mass, enclosing between them the anterior portion of the great ventral blood sinus.

The pericardium lies in the four posterior segments of the body, and is delimited ventrally from the general body-cavity by a double row of large characteristic pericardial cells. These cells have a fine homogeneous structure and are readily distinguished from the adjacent adipose tissue cells, whose size they do not attain. The pericardial cavity contains a profuse supply of fine tracheal vessels which indicates a respiratory function. A similar condition occurs in the blow-fly larva, and Imms (1907) has described a rich pericardial tracheal supply in the larva *Anopheles maculipennis*, as also Vaney (1902) and Dell (1905) in the larva of *Psychoda punctata*. The adipose tissue cells (fig. 28, *f. c.*) form the very prominent "fat-body." They are arranged in folded cellular laminae that lie chiefly in the dorso-lateral regions of the body, and in section have the appearance shown in the figure. The cells have a similar structure to those of the adult fly; they are

very large, with reticular protoplasm containing fat globules, and there may be more than one nucleus in a single cell. As in the fly, the fat-body is closely connected with the tracheal system by means of a very rich supply of tracheæ.

Two chief blood-sinuses can be distinguished—the pericardial sinus, which has already been described, lying in the dorsal region in the four posterior segments, and the great ventral sinus. The latter lies between the outer sheaths of the major cephalic imaginal discs and extends anteriorly into and about the pharynx; posteriorly it encloses the ganglion and the convoluted visceral mass, above which it opens into the pericardial sinus between the pericardial cells.

The blood which fills the heart and sinuses and so bathes the organs is an almost colourless, quickly coagulable fluid, containing colourless, nucleated, amœboid corpuscles and small globules of a fatty character.

7. THE IMAGINAL DISCS.

As in other cyclorrhaphic Diptera, the imaginal discs of some of which have been described by Weismann (1864), Kunckel d'Herculais (1875-78) and Lowne, the imago is developed from the larva by means of these imaginal rudiments, which are gradually formed during the later portion of the larval life. They do not all appear at the same time, for whereas some may be in a well-developed state early in the third larval instar, others do not appear until the larva reaches its resting period or even later. The imaginal discs appear to be hypodermal imaginations though their origin is difficult to trace in all cases; in many instances they are connected with the hypodermis by means of a stalk of varying thickness. The imaginal disc or rudiment may consist of a simple or of a folded lamina of deeply-staining columnar embryonic cells, as in the wing discs, or of a number of concentric rings of these cells, as in the antennal and crural discs. They are usually closely connected with the tracheæ and in some cases are innervated by fine nerves. Although the imaginal discs

of *M. domestica* are similar in some respects to those of the blow-fly, as described by Lowne, there are several important differences, chief of which is the position of the imaginal discs of the meta-thoracic legs.

During the resting period of the larva the cephalic and thoracic discs can be distinguished, but the abdominal discs are small and not so obvious except in sections.

The cephalic discs.—The chief cephalic discs are contained in what at first appears to be a pair of cone-shaped structures in front of each of the cerebral lobes of the ganglion (fig. 24, *m. c. d.*); the cone, however, is not complete. The outer sheath of each of these major cephalic imaginal rudiments is continued dorsally, and joins the cellular structure mentioned previously (see fig. 28), thus enclosing a triangular space which is a portion of the ventral sinus. These sheaths are continued anteriorly and are connected to the pharyngeal mass, and it is through this connecting strand of tissue that the discs are everted to form the greater part of the head of the nymph. Immediately in front of the cerebral lobe is the so-called optic disc (fig. 27, *o. d.*), which in its earlier stages is cup-shaped, but later it assumes a conical form, having a cup-shaped base adjacent to the cerebral lobe. The optic disc is connected to the cerebral lobe laterally by a stalk of tissue, the optic stalk (*o. s.*), which becomes hollow later, and it is through this stalk that the optic ganglion and associated structures contained in the cerebral lobe appear to evaginate when the final metamorphosis and eversion of the imaginal rudiments takes place. The optic discs form the whole of the lateral regions of the head of the fly. The remaining portion of the head-capsule of the fly is formed from two other pairs of imaginal rudiments, the antennal and facial discs. The antennal disc (*an. d.*) lies in front of, and internal to, the optic discs. Each consists of an elongate conical structure, in which at a later stage the individual antennal joints can be distinguished. The facial discs (*f. d.*) are anterior to the antennal discs and extend to the anterior end of the conical structure containing these

three pairs of major cephalic discs, which will form the cephalic capsule.

In addition to these two other pairs of cephalic discs are found. A pair of small flask-shaped maxillary rudiments are situated one at the base of each of the oral lobes; a second pair of imaginal discs, similar in shape to the maxillary discs, is found adjacent to the hypostomal sclerite; the latter, I believe, are the labial rudiments, and will form almost the whole of the proboscis of the fly.

The thoracic discs.—In *M. domestica* there are five pairs of thoracic discs. The pro-thoracic imaginal discs (figs. 24 and 28, *pr. d.*) are attached to the anterior end of the ganglion and slope obliquely forwards; the distal end of each is attached to the body-wall on the ventral side between segments three and four. These discs develop into the pro-thoracic legs, and probably also into the much reduced pro-thoracic segment, as I was unable to discover any other rudiments corresponding to the dorsal imaginal discs of the meso-thoracic and meta-thoracic segments. Arising from the sides of the ganglion immediately behind the attachment of the pro-thoracic rudiment are the imaginal rudiments of the meso-thoracic legs and sternal region (*v. ms.*); the distal stalks of this pair of imaginal discs are attached to the body-wall at the posterior border of the fourth segment. The dorsal meso-thoracic imaginal discs, from which originate the mesonotal region and the wings, may be termed the alar or wing discs. They form a pair of flattened pyriform sacs (fig. 22, *d.ms.*), lying one on each side of the ventral side of the fifth segment and slightly external to the lateral tracheal trunk (fig. 28, *d.ms.*), to a ventral branch of which each is attached. The meta-thoracic discs consist of two pairs of small pyriform masses (fig. 22) lying immediately behind the alar discs in the intersegmental line. They are attached to a ventral branch of the lateral tracheal trunk. The anterior rudiment (*v. mt.*) is the larger, and forms the imaginal meta-thoracic leg and sternal region; in the blow-fly and *Volucella* it is interesting to note that this pair of imaginal discs is situated further

forward, and is in association with the corresponding pro-thoracic and meso-thoracic ventral discs. The smaller and more posterior disc (*d. mt.*) will develop into the remaining portion of the much reduced meta-thoracic segment, including the halteres.

Reference has already been made to other imaginal rudiments which occur in the abdominal region as circular patches of embryonic cells. The abdominal segments develop from numerous segmentally arranged plates of a similar nature, which are found during the early pupal stage.

During pupation the imaginal rudiments increase in size and are not destroyed by the phagocytes in histolysis, as is the case with most of the larval structures. The cephalic discs are evaginated by the eversion of their sacs by way of the anterior end of the larva, a cord of cells attached to the dorsal wall of the anterior end of the pharynx marking the path of eversion. A similar process takes place in the case of the thoracic imaginal discs, which, by their eversion, build up the whole of the skeletal case of the thorax and its dorsal and ventral appendages, the wings, halteres and legs.

VI. SUMMARY.

1. An account of the previous work on the breeding habits of *M. domestica* is given, which, together with the author's investigations, show that the house-fly breeds in the following substances :

Horse-manure; this is preferred by the female flies as a nidus for the eggs, and forms the chief substance in which they breed; human excrement, either in the form of isolated faeces or occurring in such places as latrines, privies and ash-pits; cow-dung; poultry excrement; also in substances contaminated or mixed with excremental products, such as bedding from piggeries and from rabbits and guinea-pigs, paper and textile fabrics which have been contaminated, as cotton and woollen garments, sacking, rotten flock-beds, straw-mattresses, cesspools; decaying vegetable substances,

such as vegetable refuse from kitchens and decaying grain ; rotten fruit, as bananas, apricots, cherries, plums, peaches and melon-slices ; in spent hops ; in waste food-stuffs, as bread moistened with milk, boiled egg, broth ; bad meat and dead animals.

2. The most important factor in the development is temperature ; a high temperature accelerates the development. Others factors concerned in the development are—the nature of the food and moisture, the effects of which are shown. Fermentation is also an important factor in development, as first shown by de Geer.

3. The shortest time occupied in the development, that is, from the deposition of the egg to the exclusion of the imago, is eight days, which period is obtained when the larvæ are incubated at a constant temperature of about 35° C. ; under unfavourable conditions the development may extend over several weeks.

4. There are three larval stages, and the shortest times obtained for the development of the different developmental stages is—egg, from deposition to hatching, eight hours ; first larval instar, twenty hours ; second larval instar, twenty-four hours ; third larval instar, three days ; pupal stage, three days.

5. House-flies usually breed from June to October, but if the necessary conditions of temperature and suitable food are present they are able to breed practically the whole year round ; these conditions are not, as a rule, satisfied during the winter months, except in such places as warm stables, etc.

6. The flies become sexually mature in ten to fourteen days after their emergence from the pupa, and they may begin to deposit their eggs as early as the fourteenth day after emergence. Each fly lays from 120–150 eggs in a single batch, and it may lay as many as six batches during its life.

7. The anatomy of the adult larva is described in the second portion of the paper. The body of the larva is considered to be composed of thirteen segments, of which the remnant of the cephalic region or pseudo-cephalon forms the

first. The apparent single second segment is considered to be of a double nature.

8. The muscular system is described in detail. It consists of: (1) A segmentally-arranged series of flattened cutaneous muscles forming an almost perfect sheath below the hypodermis; (2) the muscles controlling the cephalo-pharyngeal sclerites and pharynx; (3) the cardiac and visceral muscles. The series of muscular actions which probably takes place during locomotion is described.

9. The central nervous system is concentrated to form a single compound ganglion in which eleven pairs of component ganglia can be recognised. On the dorsal side of the anterior end of the ganglion two cerebral lobes united in the median line above the œsophageal foramen are situated; these contain the rudiments of the optic and supra-œsophageal ganglionic structures of the fly. Eleven pairs of segmental nerves arise from the ganglion, and in addition to these three pairs of lateral nerves, and also a single pair and two median unpaired dorsal accessory nerves arise. The component ganglia are surrounded by a cortical layer containing large ganglion cells; the whole compound ganglion is enclosed in a capsular sheath.

The only sensory organs are two pairs of tubercles situated on the dorsal sides of the oral lobes. By their structure they indicate an optical function.

10. The alimentary tract is very long in the larva, the ventriculus being especially elongate. It consists of pharynx, œsophagus, proventriculus, ventriculus, intestine and rectum. In addition to a pair of salivary glands, whose ducts unite to open by a single duct at the anterior end of the pharynx, and a pair of bifurcating Malpighian tubes, the larva possesses four cæca at the anterior end of the ventriculus. The ventriculus and intestine are very convoluted and are coiled up to form a complicated visceral mass.

11. The tracheal system of the adult larva consists of two longitudinal lateral tracheal trunks united by anterior and posterior commissures, and communicating with an exterior

by means of an anterior and a posterior pair of spiracles. The anterior spiracles, which do not occur in the first larval instar, are considered to be functional.

12. The vascular system consists of: (1) A dorsal vessel, the posterior region of which is swollen to form a cardiac region or "heart" which communicates with a pericardial cavity by means of three pairs of lateral ostia; (2) the great ventral sinus, which forms the body cavity; and (3) the pericardial sinns. The pericardium is well supplied with tracheæ, which may assist in respiration, as in certain other insect larvæ. The adipose tissue cells which compose the large laminae forming the fat-body are similar in structure to those of the fly.

13. Three groups of imaginal rudiments or discs can be recognised in the larva: (1) The cephalic discs, of which two appendicular pairs are situated at the anterior end of the larva and three pairs in front of the cerebral lobes of the ganglion; (2) the thoracic discs, two pairs of which are attached to the anterior end of the ventral side of the ganglion, and three pairs are connected with the lateral tracheal trunks in the fifth segment; (3) the abdominal and visceral discs.

VII. LITERATURE.

For the sake of convenience a few of the references given in Part I have been repeated here.

1902. BERLESE, A.—"L'accoppiamento della *Mosca domestica*," 'Rev. Patalog. vegetale,' vol. ix, pp. 345—357, 12 figs.
1834. BOUCHE, P. FR.—'Naturgeschichte der Insekten besonders in hinsicht ihrer ersten Zustände als Larven und Puppen,' Berlin, 216 pp., 10 pls. (*M. domestica*, pp. 65, 66, pl. v, figs. 20—24.)
1883. BRAUER, F.—"Die Zweiflüger des kaiserlichen Museums zu Wien: III. Systematische Studien auf Grundlage der Dipteren larven nebst einer Zusammenstellung von Beispielen aus Literatur über dieselben und Beschreibung neuer Formen," 'Denkschr. der Kais. Akad. der Wiss. math-naturwiss. Classe,' Wien, vol. xlvii, pp. 1—100, 5 pls.

1905. DELL, J. A.—“On the Structure and Life-history of *Psychoda sex-punctata*,” ‘Trans. Ent. Soc. London,’ pp. 293—311.
1776. DE GEER, CARL.—‘Mémoires pour servir à l’Histoire des Insectes,’ Stockholm. (*M. domestica*, vol. vi, pp. 71—78, pl. iv, figs. 1—11.)
1908. GRIFFITH, A.—“The Life-history of House-flies,” ‘Public Health,’ vol. xxi, pp. 122—127.
1904. HENNEGUY, L. F.—‘Les Insectes,’ Paris, 804 pp.
1906. HEWITT, C. G.—“A Preliminary Account of the Life-history of the Common House-fly (*Musca domestica*, L.),” ‘Manchester Mem.,’ vol. li, part i, 4 pp.
1907. ——— “The Structure, Development, and Bionomics of the House-fly, *Musca domestica*, Linn.: Part I. The Anatomy of the Fly,” ‘Quart. Journ. Mic. Sci.,’ vol. 51, pp. 395—448, pls. 22—26.
1904. HOLMGREN, N.—“Zur Morphologie des Insektenkopfes: II. Einiges über die Reduktion des Kopfes der Dipteren-larven,” ‘Zool. Anz.,’ vol. xxvii, pp. 343—355, 12 figs.
- 1896—1906. HOWARD, L. O.—“House-flies,” in ‘The Principal Household Insects of the United States,’ by L. O. Howard and C. L. Marlatt, U.S. Dept. of Agriculture, Washington, Division of Entomology, Bull. No. 4, N.S., revised ed., pp. 43—47, and figs. 13—15; and 1906, “House-flies,” revised ed., Circular No. 71, 10 pp., 9 figs.
1900. ——— “A Contribution to the Study of the Insect Fauna of Human Excrement (with especial reference to the spread of Typhoid Fever by Flies),” ‘Proc. Wash. Acad. Sciences,’ vol. ii, pp. 541—604, figs. 17—38, pls. 30, 31.
1907. IMMS, A. D.—“On the Larval and Pupal Stages of *Anopheles maculipennis*, Meigen,” ‘Journ. of Hygiene,’ vol. vii, pp. 291—318, 1 fig., pls. 4, 5.
1790. KELLER, J. C.—‘Geschichte der gemeinen Stubenfliege,’ Nurnberg, 32 pp., 4 pls.
1887. KOWALEVSKI, A.—“Beiträge zur Kenntniss der nachembryonalen Entwicklung der Musciden,” ‘Zeit. f. wiss. Zool.,’ vol. xlv, pp. 542—594, pls. 26—30.
- 1875—81. KUNCKEL D’HERCULAIS, J.—‘Récherches sur l’organisation et le Développement des Volucelles, Insectes diptères de la famille des Syrphides,’ Paris, part i.
1858. LEUCKART, R.—“Die Fortpflanzung und Entwicklung der Pupiparen. Nach Beobachtungen an *Melophagus ovinus*,” ‘Abhandl. Naturf. Gesell.,’ Halle, vol. iv, pp. 147—226, 3 pls.

1890. LOEB, J.—‘Der Heliotropismus der Thiere und seine Uebereinstimmung mit dem Heliotropismus der Pflanzen,’ Wurzburg, 118 pp., 6 figs.
- 1890-92. LOWNE, B. T.—‘The Anatomy, Physiology, Morphology, and Development of the Blow-fly (*Calliphora erythrocephala*),’ vol. i, London.
1762. LYONET, P.—‘Traite anatomique de la Chenille qui ronge le bois de Saule,’ 2nd ed., La Haye, 18 pls.
1902. DE MEIJERE, J. C. H.—‘Ueber die Prothorakalstigmen der Dipterenpuppen,’ ‘Zool. Jahrb.’ (Anat.), vol. xv, pp. 623-692, pls. 32-35.
1839. NEWPORT, G.—‘Insecta,’ in Todd’s ‘Cyclopædia of Anatomy and Physiology,’ vol. ii, pp. 853-994.
1907. NEWSTEAD, R.—‘Preliminary Report on the Habits, Life-cycle, and Breeding Places of the Common House-fly (*Musca domestica*, Lin.) as observed in the City of Liverpool, with suggestions as to the best means of checking its increase,’ Liverpool, 23 pp., 14 figs.
1874. PACKARD, A. S.—‘On the Transformations of the Common House-fly, with notes on allied forms,’ ‘Proc. Boston Soc. Nat. Hist.,’ vol. xvi, pp. 136-150, 1 pl.
1738. REAUMUR, R. A. F. DE.—‘Mémoires pour servir à l’Histoire des Insectes,’ vol. 4. (*M. domestica*, p. 384.)
1862. SCHINER, J. R.—‘Fauna Austriaca: Die Fliegen,’ Wien., vol. i, 674 pp.
1907. SMITH, F.—‘House-flies and their ways at Benares,’ ‘Journ. Roy. Army Med. Corps,’ vol. ix, pp. 150-155 and p. 447.
1880. TASCHENBERG, E. L.—‘Praktische Insektenkunde,’ part iv (*M. domestica*, pp. 102-107, fig. 27).
1902. VANEY, C.—‘Contributions à l’étude des Larves et des metamorphoses des Diptères,’ ‘Ann. de l’Univ. de Lyon,’ N.S., I. Sciences-méd., fasc. 9, 178 pp., 4 pls.
1901. VIGNON, P.—‘Recherches de Cytologie générale sur les Epitheliums, l’appareil pariétal protecteur ou moteur; le rôle de la co-ordination biologique,’ ‘Arch. Zool. Exp. et Gen.,’ vol. ix, pp. 371-720, pls. xv-xviii.
1863. WEISMANN, A.—‘Die Entwicklung der Dipteren im Ei, nach Beobachtungen an *Chironomus spec.*, *Musca vomitoria* und *Pulex canis*,’ ‘Zeit. f. wiss. Zool.,’ vol. xiii, pp. 107-220, pls. vii-xiii.
1864. ——— ‘Die nachembryonalen Entwicklung der Musciden nach Beobachtungen an *Musca vomitoria* und *Sarcophaga carnaria*,’ ‘Zeit. f. wiss. Zool.,’ vol. xiv, pp. 185-336, pls. xxi-xxvii.

EXPLANATION OF PLATES 30—33,

Illustrating Mr. C. Gordon Hewitt's paper on "The Structure, Development, and Bionomics of the House-fly *Musca domestica*, Linn. Part II. The Breeding Habits Development and the Anatomy of the Larva."

PLATE 30.

FIG. 1.—Eggs of *M. domestica*, $\times 40$, dorsal and dorso-lateral views.

a. Anterior end.

FIG. 2.—Egg immediately before emergence of the larva which can be seen through the dorsal split of the chorion through which it emerges.

FIG. 3.—Posterior end of mature larva (3rd instar).

an. Anus. *p.sp.* Posterior spiracle.

FIG. 4.—Cephalopharyngeal skeleton of mature larva, left lateral aspect.

d.p.s. Dorsal pharyngeal sclerite. *d.s.* Dentate sclerite, *h.s.* Hypostomal sclerite. *l.p.* Lateral pharyngeal sclerite or plate, deeply incised posteriorly to form dorsal and ventral processes. *m.s.* Mandibular sclerite.

FIG. 5.—Mature larva of *M. domestica*.

a.sp. Anterior spiracular process. *an.l.* Anal lobe. *sp.* Spiniferous pad. I—XIII. Body segments.

FIG. 6.—Ventral aspect of the Pseudocephalon and second body segment of the mature larva showing the two oral lobes traversed by the food channels.

l. Lingual-like process. *m.* Mouth. *m.s.* Mandibular sclerite. *o.t.* Anterior optic tubercle.

FIG. 7.—Transverse section through two of the papillæ of the anterior spiracular process to show the clear central lumen.

c.p. The cuticular processes.

FIG. 8.—Larva shortly after hatching (1st instar).

m.s. Mandibular sclerite. *p.sp.* Posterior spiracle raised on short tubercle. *sp.* Spiniferous pad.

FIG. 9.—Lateral (left) aspect of the anterior end of the mature larva.

I—IV. Body segments. *a.sp.* Anterior spiracular process showing seven spiracular papillæ. *m.s.* Mandibular sclerite. *o.t.* Optic tubercle. *ps.* Pseudocephalon.

FIG. 10.—“Nymph” of *M. domestica* dissected out of pupal case about 30 hours after pupation.

an. Swellings of nymphal sheath marking bases of antennæ. *cx.* Coxa of leg. *lb.* Labial portion of proboscis sheath. *lbr.* Labral portion of same. *n.sp.* Spiracular process of nymph. *w.* Wing in nymphal alar sheath.

FIG. 11.—Head of “nymph” (about 48 hours after pupation). Enclosed in nymphal sheath. To show the development of the imaginal proboscis.

an. Antenna. *c.e.* Compound eye. *fac.* Facialia. *lab.* Labrum. *mx.p.* Maxillary palp. *o.l.* Oral lobe.

FIG. 12.—Posterior end of larva in the second stage (2nd instar).

an. Anus. *p.sp.* Posterior spiracle.

FIG. 13.—Cephalopharyngeal skeleton of the first larval instar; the outline of the pharyngeal mass is shown in dotted lines.

l.s. T-shaped sclerite of the left oral lobe. Other lettering as in Fig. 4.

FIG. 14.—Longitudinal section through the surface of one of the oral lobes of mature larva to show the food-channels.

ch. Food-channel. *ct.* Outer layer of cuticular integument. *ct'.* Inner layer of the same. *hy.* Hypodermis.

FIG. 15.—Pupal case of *M. domestica* from which the imago has emerged, thus lifting off the anterior end or “cap” of the pupa; ventro-lateral aspect.

a.sp. Remains of the anterior spiracular process of larva. *l.tr.* Remains of the larval lateral tracheal trunk. *n.sp.* Temporary spiracular process of nymph. *p.sp.* Remains of the posterior spiracles of larva.

PLATE 31.

FIG. 16.—Muscular system of the body-wall of the right side. The straight dorsal line is the median dorsal line of the body, and the curved ventral line is the median ventral line.

I—XIII. Body segments. *an.l.* Anal lobe. *an.m.* Anal muscle. *c.r.* Cephalic retractor muscle. *d.v.* Dorso-ventral muscle of the terminal segment. *ex.d.l.* External dorso-lateral oblique recti muscles. *i.l.o.* Internal lateral oblique muscle. *in.d.l.* Internal dorso-lateral oblique recti muscles. *l.i.m.* Lateral intersegmental muscle. *l.m.* Lateral muscles. *l.tr.* Branch of lateral tracheal trunk communicating with the anterior spiracular process. *l.v.l.* Longitudinal ventro-lateral muscles. *p.sp.* Posterior spiracle. *s.d.* Stomal dilators. *v.c.r.*, *v'.c.r.* Ventral cephalic retractor muscles. *v.l.o.* Ventro-lateral oblique muscle. *v.o.* Ventral oblique muscle.

FIG. 17.—Oblique section through the pharyngeal mass of the larva in the direction and at the level shown by the line *a.b.* in Fig. 19. (Camera lucida drawing.)

e.o.m. Elongate oblique pharyngeal muscle. *l.p.* Lateral pharyngeal

sclerite. *m.* Accommodating membrane. *m.d.* Mandibular depressor muscle. *o.ph.* Oblique pharyngeal muscle. *ph.* Pharynx. *s.d.m.* Semicircular dorsal pharyngeal muscles. *tr.* Trachea. *v.c.p.* Ventral cephalic protractor muscle.

FIG. 18.—Oblique section through the pharyngeal mass of the larva at the level shown by the line *x.y.* in Fig. 19. (Camera lucida drawing.)

p.s. Pharyngeal sinus. *r.ph.* Roof of pharynx. *T.r.* T-ribs of the floor of pharynx. Other lettering as in Figs. 17 and 19.

FIG. 19.—Muscles of the cephalo-pharyngeal sclerites of the mature larva seen from the left side. The muscles of the body-wall have been omitted with the exception of the large cephalic retractor muscles.

a.b., x.y. Levels and direction of the oblique sections shown in Figs. 18 and 19. *c.r.* Cephalic ring. *d.c.p.* Dorsal cephalic protractor muscle. *d.m.* Right pharyngeal depressor muscle. *d.s.* Dentate sclerite. *f.p.* Chitinous floor of the posterior region of the pharynx showing the bases of the T-ribs. *h.s.* Hypostomal sclerite. *m.d.* Mandibular depressor muscle. *m.e.* Mandibular extensor muscle. *m.s.* Mandibular sclerite. *s.d.* Stomal dilator muscles. *sal.d.* Common salivary duct. *v.c.p.* Ventral cephalic protractor muscles. *v.c.r.* and *v'.c.r.* Ventral cephalic retractor muscles.

FIG. 20.—Visceral or stomatogastric nervous system of the mature larva. The position of the ganglion (*G.*) with the cerebral lobes (*c.l.*) is shown by means of the dotted outline.

c.g. Central visceral ganglion. *pv.g.* Proventricular or posterior ganglion.

FIG. 21.—Transverse section of one of the salivary glands of the mature larva. (Camera lucida drawing.)

FIG. 22.—Internal aspect of the posterior thoracic imaginal discs of the right side.

d.ms. Dorsal mesothoracic or alar imaginal disc. *d.mt.* Dorsal metathoracic imaginal disc. *l.tr.* Lateral tracheal trunk of the right side of larva. *v.mt.* Ventral metathoracic imaginal disc.

PLATE 32.

FIG. 23.—Nervous system of the mature larva. The dorsal accessory nerves are shown by single black lines, and the outline of the pharyngeal mass is indicated by the dotted line.

I—XIII. Body segments of the larva. *c.l.* Cerebral lobes. *m.c.d.* Major cephalic imaginal discs. *œ.* Œsophagus. *o.v.* Anterior (œsophageal branch) of visceral nervous system.

FIG. 24.—Left lateral aspect of the ganglion of the mature larva showing the origin of the nerves, position of the imaginal discs, and anterior end of the dorsal vessel.

1—11. Eleven segmental nerves. *a.b.* and *c.* Nerves arising from the bases

of the stalks of the prothoracic and ventral mesothoracic imaginal discs. *c.l.* Cerebral lobe. *c.r.* Problematical cellular structure (Weismann's "ring"). *d.a.*, *d.a'*, *d.a''*. Dorsal accessory nerves. *d.v.* Dorsal vessel. *m.c.d.* Major cephalic imaginal discs. *æ.* Œsophagus. *pr.d.* Prothoracic imaginal disc. *l.* Fine tracheæ which arise in association with the segmental nerves, others arise with some of the more posterior nerves, but for the sake of clearness they are not included in the figure. *tr'*, *tr''*. Tracheæ entering the ganglion. *v.m.s.* Ventral mesothoracic imaginal disc. *v.n.* Visceral nerve.

FIG. 25.—Longitudinal section of the proventriculus of the mature larva (Camera lucida drawing.)

c.c. Large cells forming the central hollow core of the proventriculus. *ch.i.* Chitinous intima of the œsophagus. *e.v.* Epithelial cells continuous with and similar in character to those of the ventriculus. *i.c.* Ring of imaginal cells. *æ.ep.* Œsophageal epithelial cells. *v.c.* Lumen of ventriculus.

FIG. 26.—The longitudinal lateral tracheal trunk of the left side seen latero-dorsally showing the origin of the tracheal branches; small portions only of the right trunk are shown.

a.com. Anterior tracheal commissure. *a.sp.* Anterior spiracular process. *f.b.* Fat-body. *or.l.* Oral lobe. *l.tr.* Longitudinal lateral tracheal trunk. *p.com.* Posterior commissure. *p.sp.* Posterior spiracle. *tr'*. Trachea entering ganglion anteriorly. *tr''*. Trachea entering ganglion laterally. *v.tr.* Visceral tracheal trunk.

FIG. 27.—Longitudinal sections through the major cephalic imaginal discs of mature larva to show the position of the individual imaginal rudiments. The dextral section is more dorsal than the sinistral. (Camera lucida drawings.)

an.d. Imaginal disc of the antenna. *f.d.* Facial imaginal disc. *i.s.* Sheath of imaginal rudiments. *o.d.* Optic imaginal disc. *o.g.* Imaginal disc of the optic ganglionic structures. *o.s.* Optic stalks. *s.g.* Fundament of the imaginal supra-œsophageal ganglionic. *sh.* Sheath of cerebral lobe.

FIG. 28.—Transverse section of mature larva anterior to the ganglion and cerebral lobes to show the position of certain of the imaginal discs. The body-wall and muscles have been omitted. The folded character of the adipose tissue laminæ can be seen in this section, and also the degenerating anterior portions of the malpighian tubules (*m.t.*). (Camera lucida drawing.)

an.d. Antennal disc. *c.r.* Problematical cellular structure (Weismann's "ring"). *c.v.* Cæcum of ventriculus. *d.ms.* Dorsal mesothoracic (alar) imaginal disc. *f.c.* Adipose tissue cell. *l.tr.* Lateral tracheal trunk. *m.t.* Malpighian tubule cut rather longitudinally. *æ.* Œsophagus. *pr.d.* Prothoracic imaginal disc. *v.ms.* Ventral mesothoracic imaginal disc.

PLATE 33.

FIG. 29.—Alimentary system of mature larva. The course of the ventriculus and intestine as they lie in the larva is shown by the dotted lines. The origins only of the Malpighian tubes are shown.

c.s.d. Common salivary duct. *c.v.* Cæcum of ventriculus. *int.* Intestine. *m.t.* Malpighian tubule. *œ.* Œsophagus. *ph.* Pharynx. *pv.* Proventriculus. *r.* Rectum. *s.gl.* Salivary gland. *v.* Ventriculus.

FIG. 30.—Transverse section of a portion of the ventriculus of mature larva. (Camera lucida drawing.)

e.v. Epithelial cell of ventriculus showing large active nucleus and striated peripheral region of cell. *g.s.* Probable gland cells. *i.c.* Group of imaginal cells.

FIG. 31. Horizontal section of posterior or "cardiac" region of the dorsal vessel. (From camera lucida drawings.)

os. Ostium. *v.* Valvular flaps guarding the same.